THE NATURE OF BUD VARIATIONS AS INDICATED BY THEIR MODE OF INHERITANCE[1]

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THE title limits this account to such bud variations as have been studied critically with respect to their inheritance in sexual reproduction. The further limitation of time makes it necessary that I choose from among such studies certain cases to serve as illustrations of the several types of bud variation. I shall, therefore, attempt no complete review of the researches bearing on the problem at hand.

A survey of published accounts of bud-variation studies shows that as yet comparatively little is definitely known of the real nature of these vegetative sports. It seems not unlikely, however, that to point out some of the problems suggested by these studies and, where possible, to note modes of attack may serve the purpose of this symposium quite as well as a rehearsal of known facts and their interpretation.

As here used, the term bud variation is synonymous with vegetative as contrasted with seminal variation. The term somatic variation may also be employed to the same effect, provided it is not thereby intended to exclude cases in which the germ tract as well as the soma is involved. At the outset, however, there must be imposed on any of these terms, for the purpose of this discussion at least, the limitation that the variation involves a change in the genetic constitution of the parts affected.

The expressions somatic mutation and somatic segregation are specific terms and as such are not to be used interchangeably with the more general terms somatic, vegetative, or bud variations. Moreover, to speak of a particular vegetative variation as a case of somatic muta-

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tion or of somatic segregation without basis from critical inheritance or cytological studies is to prejudge the nature of the observed modification.

Frequency of Somatic Variations

Attempts have been made to estimate the relative frequency of vegetative and seminal variations in plants, but little definite information has been gained. The problem is beset with grave difficulties inherent in most attempts to determine coefficients of mutability. The possibility of overlooking even prominent variations until they have once been noted, together with the readiness with which they are found after one's attention has been focused on them, will hardly be questioned by anyone who has given attention to the discovery of new variations in almost any organism. One may attempt with some assurance an estimation of the frequency of recurrence of a particular mutation, for instance, whether it appears in vegetative parts of individuals or in sexually produced progenies, but it is a hazardous undertaking to estimate the frequency of variations in general. Until some one can devise a scheme for estimating the frequency of bud variations as Muller has done for determining mutation frequencies in *Drosophila*, little progress can be looked for other than through investigations of the somatic mutation or segregation of specific genes.

The problem of the relative frequency of occurrence of somatic and gametic variations meets the further difficulty that it is often impossible to determine the ontogenetic stage at which particular variations have arisen—a fact that has been noted for plants by various writers (deVries, 1910; Emerson, 1913; East, 1917). Both Bridges (1919) and Muller (1920) have discussed this problem from the standpoint of studies of particular mutations in *Drosophila*. The prevalent opinion that variations arise in the gametes or at about the time of their formation may have come in part from a belief that aberrant chromosome behavior is most likely to occur at the time of the reduction division. It seems likely, however, that the situation has been confused by failure to realize

that recessive mutations—the most frequent kind—can not be expressed in the individual in which they occur except when the dominant allelomorph is simplex, while such mutations may appear in a later generation of sexually produced progeny (East, 1917).

SOMATIC MUTATION OF GENES

Several cases of vegetative variation in plants have been studied with sufficient thoroughness to leave little doubt that they are mutations in the strict sense, involving the modification of particular genes. Most of them are concerned with variegated color patterns of flowers, leaves, or fruits, and they are more or less regularly recurrent, a fact that makes them especially well suited to quantitative studies, for it is obvious that a quantitative study can be made only of variations that occur with considerable frequency. For the most part also these somatic mutations are dominant to the type from which they spring, appearing frequently in material homozygous for their recessive allelomorphs, facts that exclude the possibility of their being due to any sort of somatic segregation of unlike genes. Blakeslee's (1920) case of a somatic variation in *Portulaca* is one of the few examples not involving variegation. Other cases have been reported by Baur (1918).

One of the earliest cases of somatic mutation was reported by deVries in variegated flowers of *Antirrhinum*. Though the work was done prior to the rediscovery of Mendelism and not discussed from the standpoint of recent genetic interpretation, there is little doubt, as I have noted elsewhere (Emerson, 1913), that the results can best be interpreted as due to a somatic gene mutation.

Correns's (1910) results with respect to the occurrence and behavior in inheritance of green-leaved variations on variegated-leaved *Mirabilis* and of self-colored flowers on variegated flowered strains of the same species were among the first to be subjected to critical genetic analysis. The behavior in inheritance of green branches of variegated *Mirabilis* shows this vegetative variation to be a simple dominant mutation affecting ordinarily only one of the duplex recessive allelomorphs. A mutated branch

is, therefore, as truly a heterozygote as if it had arisen through hybridization of green and variegated strains.

Self-colored branches on variegated-flowered plants of *Mirabilis* usually do not transmit the self-color character to their seed progenies in greater percentages than do variegated-flowered branches of the same plants. They are thought by Correns to be fundamentally of the same nature as the green branches of variegated-leaved plants, their failure to transmit the self-color character being due presumably to the accident that the mutation occurs in epidermal cells from which no gametes arise. The frequent occurrence of self-colored plants in seed progenies both of self-colored and of variegated flowers is considered evidence of their origin as vegetative rather than as gametic mutations, their failure of expression in the soma being thought due to their origin in sub-epidermal cells in which these flower colors do not develop.

Studies of variations in variegated pericarp of maize by myself (Emerson, 1914, 1917) and by Anderson, Eyster, and Demerec,[2] involve practically the same results as those so far reported in investigations of other species and afford in addition quantitative data on certain aspects of the somatic-mutation problem not included in other investigations. The genes for variegated pericarp have been shown to belong to a comparatively large series of multiple allelomorphs including those for colorlessness (white seeds), self color of different intensities, and certain definite color patterns of both the pericarp of the seeds and the glumes and paleæ of the cobs. Variegation is known to be a simple recessive to self color and a dominant to white.

Self-colored seeds whether occurring singly or in groups in variegated ears produce progenies consisting of approximately 50 per cent. self-colored ears, the other 50 per cent. being either all variegated or all white depending on whether the parent was homozygous variegated, *V V*, or heterozygous variegated, *V W*, from a previous cross with white. Seeds that are less than wholly self colored throw a correspondingly smaller per cent. of

[2] Unpublished data by W. H. Eyster and E. G. Anderson, and by E. G. Anderson and M. Demerec.

self-colored ears. Self-colored seeds thus produced have, so far as tested, proved to be heterozygous for self color, behaving in later generations exactly as if produced by crosses of self-colored with variegated or with white races.

Certain cultures of self-colored maize produce a few variegated seeds. Such seeds have been observed only on ears that are heterozygous from previous crosses with variegated strains, *S V*, or with white strains, *S W*, never from ears that are homozygous for self color, *S S*. From such variegated seeds, new variegated races have been produced.

These facts are regarded as indicating (1) that the occurrence of self-colored or partly self-colored seeds on variegated ears is due to somatic mutations of the recessive variegation gene to the dominant self-color allelomorph; (2) that only one of the two variegation genes of homozygous variegated maize mutates at a given time; (3) that it is always the variegation gene, never the white one, of heterozygous material that mutates; (4) that the occurrence of variegated seeds on otherwise self-colored ears is due to reverse mutations from the dominant self-color gene to the recessive variegation allelomorph; and (5) that only one of the duplex genes of self-color strains so mutates at any one time, for otherwise there would remain no dominant self-color gene to prevent the expression of the mutation as variegated seeds in homozygous self-colored material.

Another type of somatic variation, quite distinct from the self-color mutations discussed above and often termed dark-crown variation, also occurs frequently in variegated maize pericarp (Emerson, 1917). It is quite as striking in appearance as the self-color mutation, but is not inherited, the progenies of the aberrant seeds being in no way different from those of the normal seeds of the same ears. Microscopic examination of dark-crown and of self-color seeds indicates that in the former the epidermis alone is colored while in the latter the epidermis alone remains colorless. The conclusion seems warranted, therefore, that the two types of variation are fundamentally the same, both being true gene mutations, and

that the non-inheritance of the dark-crown type is due to the accident that it occurs in epidermal tissue outside the germ tract.

Recent investigations of variegated maize by Eyster and Anderson have established the fact that somatic mutations affecting small areas occur much more frequently than those affecting large areas. Since a mutation arising in a single cell late in development obviously could not affect so large an area as one originating earlier, it follows that mutations in variegated maize occur with increasing frequency in the later stages of ontogeny. It is true, as pointed out by Muller (1920), that given a constant rate of mutation throughout all stages of ontogeny and granting that one cell is as likely as another to mutate, mutations should appear more frequently in the later stages of development because of the fact that there are then many more cells in which mutations may arise. But Eyster and Anderson have found that the increase in the frequency of occurrence of mutations during the progress of development is accelerated far beyond expectation based on the increase in number of cells.

This behavior is strongly suggestive of a progressive acceleration in the mutability of the variegation gene as development proceeds. It is much too early to say whether this progressive change, if such it be, is inherent in the organization of the gene itself, as suggested by Anderson and Demerec, or whether it is a response to progressive changes in physiological and environmental relations. Perhaps the assumption of an equal chance of mutation as between any two cells is without sufficient warrant. Possibly there is a time element to be taken into account, as noted by Muller (1920). As cell division becomes progressively retarded in the late growth stages, may not each cell be exposed for an increasingly longer period of time to the chance of mutation? Perhaps it may be possible to test this assumption in favorable material by a comparison of the frequency of mutation in the very early slow-growth, the later rapid-growth, and the final slow-growth periods of the life cycle; but the relatively few cells present in the very early growth period seems likely to place serious limitations on the

practicability of such a test. An observation of possible importance in connection with the question of a time element in mutation and with the problem of environmental and physiological influences is that made by Eyster and Anderson concerning the greater frequency of the non-heritable (epidermal) mutations than of the heritable (sub-epidermal) ones in variegated pericarp of maize.

I have recently obtained results bearing on another phase of the somatic-mutation problem as related to variegated maize pericarp, namely, the relative frequency of mutation of homozygous, *V V*, and of heterozygous, *V W*, material. It has been shown above that the *W* gene for colorless (white) pericarp does not mutate, so far as known, when paired either with itself, *W W*, with the variegation gene, *V W*, or with the self-color gene, *S W*. It will be recalled further that only one of the two homologous genes in homozygous variegated, *V V*, material mutates at any one time. If it could be assumed that the mutability of either allelomorph is uninfluenced by the presence of the other, it should follow that somatic mutations will occur with approximately twice the frequency in homozygous, *V V*, as in heterozygous, *V W*, material. But this expectation has not been realized. On the contrary, both heritable (self-color) and non-heritable (dark-crown) mutations have appeared throughout all my cultures with somewhat greater frequency in heterozygous than in homozygous variegated ears. The difference has been especially pronounced in very light variegated strains, where mutations have appeared about two and one half times as often in heterozygous as in homozygous material. Even if mutations appeared with equal frequency in heterozygous and in homozygous ears, the simplex gene of the former must have a mutability of about twice that of either of the duplex genes of the latter. In the very light variegated strains, therefore, a simplex gene must have a mutability of about five times that of a duplex gene.

What appears to be a similar result in *Mirabilis* has been reported by Correns (1903, 1904). Crosses of a supposedly pure white race with several self-colored pink yellow, and pale yellow races resulted in every case in

plants with strongly red-striped flowers and with numerous self red flowers or even whole branches of such flowers. Intercrosses of the pink and yellow races gave only self-colored progeny, from which fact it was concluded that the white-flowered race carried a latent factor for striping. It was later discovered that about three per cent. of the flowers of the white race showed minute flecks of red. It was evidently an extremely light, variegated race, rarely if ever throwing somatic self-color mutations when the variegation gene was duplex (homozygous material) but producing such mutations with considerable frequency when that gene was simplex (heterozygous material). Correns concluded that red variegation of *Mirabilis* flowers is a character that, with self-fertilization or inbreeding, remains almost completely latent, but which, through the entrance of foreign germ plasms, is brought to full expression.

If the mutability of a gene can be increased through the influence of some modifying factor or factors brought into combination with it by crossing, as suggested by Correns, it should be possible to discover crosses that would not produce the effects so far observed in *Zea* and *Mirabilis*. While the problem deserves much more study from this viewpoint, it seems unlikely that results with maize can be explained on any such basis, unless the postulated modifying factor is the allelomorph of the variegation gene or some factor very closely linked with it. It must be noted in this connection that the comparison in maize was made between homozygous and heterozygous variegated ears of the same F_2 progenies grown from self-pollinated F_1 heterozygotes—a circumstance that would afford abundant opportunity for recombinations of independently inherited modifying factors. That the differences in mutability noted in maize may be due to differences in the interaction of like as contrasted with that of unlike allelomorphs, as suggested by Anderson and Demerec, is a somewhat novel conception worth careful consideration if means can be devised for subjecting it to a crucial test.

Before the topic of somatic mutation is dismissed, it should be noted that the phenomenon is not limited to

plants. Among animals, *Drosophila* (Morgan and Bridges, 1919) has furnished several examples of undoubted somatic mutation resulting in mosaic individuals other than gynandromorphs.

Somatic Segregation

Bud variations have probably been ascribed to somatic segregation more frequently than to any one other cause. Perhaps the opinion commonly held that bud variations occur more frequently in hybrids than in other material and the long known fact that seed-grown offspring of hybrids exhibit segregation, is chiefly responsible for this usage. It is, of course, possible that most vegetative variations are of this nature, but the fact that the individuals in which they arise are frequently found to be heterozygous for the genes concerned is no conclusive evidence that segregation is involved. Mutations also, as noted by several writers, are most likely to appear in heterozygous material because most of them are recessive and the unmutated dominant allelomorphs prevent their expression in the individuals in which they originate if the latter are homozygous.

Chromosome Elimination.—The best examples of somatic segregation that have been subjected to critical genetic analysis are afforded by the work with *Drosophila*. It has been shown by Morgan and Bridges (1919) that, of the relatively numerous gynandromorphs which have appeared in the course of investigations with *Drosophila*, nearly all have resulted from the elimination of the sex chromosome at some early cleavage division. If a fertilized egg starts as a female, XX, and one X chromosome is eliminated at an early segmentation that part of the individual developing from the cell that receives but one X chromosome should be male, XO, while the remaining part should be female, XX.

The evidence in support of this view was obtained from crosses the parents of which had different sex-linked and different autosomal characters, that is, characters whose genes are carried by the sex chromosomes and by the autosomes, respectively. The male, as well as the female,

side of gynandromorphs appearing in such crosses exhibited all the dominant autosomal characters whether they came from the maternal or the paternal parent. When the mother had a recessive, mutant gene in one of her autosomes and the father had its dominant, normal allelomorph, the fact that the male side of gynandromorphs did not have the maternal, recessive autosomal character effectively disposed of Boveri's hypothesis of partial fertilization. On the other hand, when a recessive autosomal gene entered from the father's side and its dominant allelomorph from the mother's side, the fact that the male side of the gynandromorphs did not show the paternal, recessive character likewise eliminated Morgan's earlier hypothesis of polyspermic fertilization. It has been shown, further, from crosses, the parents of which differed in sex-linked characters, that maternal and paternal X chromosomes are eliminated with about equal frequency.

In certain experiments with *Drosophila,* in which a determination of the frequency of sex-chromosome elimination was undertaken, it was found that one gynandromorph appeared in about every 2,200 individuals. Since only those individuals that start as females give the kind of gynandromorphs observed in these tests, it was concluded that one case of chromosome elimination occurs in about 1,100 individuals.

Of the evidence from plant material there is the recent account by Frost (1921) of the occurrence of a bud sport in *Matthiola* in which presumably linked genes have segregated out simultaneously in one or more branches. While this case will require further investigation before the manner of its origin can be positively established, it seems probable that it belongs to the category of somatic segregation by chromosome elimination or non-disjunction.

Studies of mosaic endosperm of maize afford perhaps the most definite evidence available in plants that certain somatic variations are due to aberrant chromosome behavior such as non-disjunction or elimination (Emerson, 1921). The genetic evidence that I have been able to obtain in support of this interpretation is of much the same

nature as that noted above for *Drosophila* gynandromorphs. In crosses in which recessive aleurone and endosperm characters are contributed by the female parent and their dominant allelomorphs by the male parent, spots of the recessive (maternal) aleurone color are underlaid by the recessive (maternal) type of endosperm when the genes for these aleurone and endosperm characters are genetically linked, that is, when they are carried in the same chromosome. On the contrary, similar recessive (maternal) aleurone-color spots are always underlaid by the dominant (paternal) type of endosperm when the genes are not linked, that is, when they are carried in non-homologous chromosomes. The fact that linked genes separate out simultaneously while non-linked ones do not do so supports the view that mosaic seeds are the result of some chromosome aberration such as elimination or non-disjunction, and renders untenable the earlier hypotheses of incomplete fusion of endosperm nuclei suggested by Correns and by Webber and also that of gene mutation proposed by myself.

The work with aberrant maize endosperm has furnished an opportunity to study the frequency of chromosome aberrations in a specialized tissue. The available data show that when a single chromosome alone is concerned, about one mosaic seed occurs in every 420 seeds. If the other two homologous chromosomes of any one set are involved as frequently and if any one of the ten triploid chromosome sets is as likely to be involved as any other one, one case of aberrant chromosome behavior should occur in about every fourteen seeds. There is some evidence, though not convincing as yet, that in different strains of maize chromosome aberrations may occur with strikingly different frequencies. In one culture in which only a single chromosome could have been involved in the origin of mosaic seeds, as many as twenty-five such seeds have been observed on a single ear of approximately 500 seeds, or one for each 20 seeds. If this behavior proves to be a constant one in this strain and if the other 29 chromosomes behave in like manner, it should furnish excellent material for cytological investigation. Moreover, the possibility of the existence of

strains of maize differing so widely in the frequency of chromosome elimination or non-disjunction raises interesting questions concerning the causes of such aberrations. It would seem possible to determine by appropriate tests something as to the relative influence of maternal and of paternal contributions on the rate of chromosome elimination.

There are circumstances connected with these results from *Drosophila* and *Zea* that may raise some doubt of their general applicability to cases of bud variation. The *Drosophila* evidence is limited almost exclusively to the sex chromosomes, though there is no positive evidence that elimination may not occur among autosomes and result in non-viable individuals. The data from *Zea* relates to endosperm alone, a specialized, nutritive, sterile, triploid tissue. There is perhaps justification for a belief that the sex chromosomes of animals and the triploid chromosomes of the endosperm of angiosperms may be subject to irregularities in behavior not commonly found in other material. The only answer to such a contention is (1) that gynandromorphs and endosperm mosaics are the materials that have been critically studied and (2) that there is, or should be, no presumption in favor of vegetative segregation through chromosome elimination or through other means as against vegetative mutation or any other mechanism as a possible explanation of bud variations that have not been subjected to cytological investigation or to critical genetic analysis.

Cytoplasmic Segregation.—Numerous cases of apparent segregation of cytoplasmic elements have been reported in plants. Of these, examples from *Mirabilis, Pelargonium, Primula,* and *Zea* may be noted. All of them involve visible effects on chlorophyll development and all show non-Mendelian inheritance.

Correns (1909*a, b*) working with a white-spotted-leaved type of *Mirabilis* observed a very irregular distribution of the white and green areas, each varying from small spots to whole branches. These white and green characters were found to be inherited through the mother only. The situation with respect to *Pelargonium,* re-

ported by Baur (1909), differs from that in *Mirabilis* in that the spotting is transmitted through the pollen as well as through the egg cells. Spotting appeared in F_1 in crosses of white with green without respect to which way the cross was made. As in *Mirabilis,* wholly white and wholly green, as well as mosaic, branches were observed.

Examples of maternally inherited chlorophyll variegation have been investigated by Gregory (1915) in *Primula,* and by Anderson[3] in *Zea.* The genetic behavior of these materials is quite the same as that of Correns's *Mirabilis* variegation. The apparent difference in the cytological basis of their behavior, however, must not be overlooked.

Evidently these plants of *Mirabilis, Pelargonium, Primula,* and *Zea* are sectorial chimæras. Their main interest in connection with this discussion lies in the fact that, starting with a single fertilized egg cell, certain chlorophyll deficiencies are apparently separated out into certain vegetative cells and handed on through definite cell lines, while normal chlorophyll develops in other cell lines, with the result that areas of varying extent have one or the other of these characters. In what the mechanism of this segregation consists—if segregation it be—is not in all cases certainly known. It may even be that some cases of variegated chlorophyll are to be regarded as recurrent variations arising *de novo* after the manner of somatic mutations but effecting changes in the cytoplasm, or some of its inclusions, rather than in the chromosomes. Baur is inclined to the view that in mosaic plants of *Pelargonium* deformed chloroplasts are responsible for the chlorophyll deficiencies and that these are segregated out by chance in cell division. This view is supported by Gregory, who noted in the young leaves of variegated plants of *Primula* the existence of normal and chlorotic plastids in the same cells. Correns does not commit himself to any particular element or inclusion of cytoplasm as the seat of the cause of chlorophyll deficiency. Randolph (1922), from cytological examination of Anderson's striped leaved maize, found that, in the

3 Unpublished data.

transition regions between the green and the pale-green areas, the cells contain not only green and colorless plastids, but all intermediate conditions as well. Since the green and the white plastids are not two sharply differentiated kinds, but are the end members of a continuous series arising from minute primordia which, so far as can be seen, are of one kind, he regards any simple form of segregation hypothesis as inadequate. It seems possible, however, that these primordia may be functionally, even though not morphologically, of two more or less distinct classes.

Graft-hybrids and Other Chimæras.—The well-known graft-hybrids of *Solanum* reported by Winkler are of interest from the standpoint of this discussion because of the bud variations commonly exhibited by them. Sectorial chimæras, produced by adventitious buds arising from the point of union of stock and scion of grafts of tomato and nightshade, and having one side of the one species and the other side of the other, have not infrequently later produced branches that were periclinal chimæras having tissues of one species enclosed within an envelope of the other. That these branches are really periclinal chimæras has been established by chromosome counts and by the fact that seedlings produced by them are always of the species of the subepidermal tissue from which gametes arise. These periclinal chimæras in turn have been observed to produce branches wholly of one or other of the parent species. The marked difference in appearance between the sectorial and periclinal chimæras and between the latter and either parent species places this behavior clearly in the class of bud variation and, since the production of branches of the parent species from periclinal chimæras is the result of a separation of genotypes that were closely united previously, the phenomenon is perhaps rightly classed as a form of vegetative segregation. It is obvious, however, that the separation of tissues that are merely closely associated in the graft hybrid is a fundamentally different type of segregation from that by which the chromosomes or even the

plastids or other cytoplasmic elements of a single cell are dissociated.

The behavior of "natural" periclinal chimæras of *Pelargonium*, noted by Baur (1909), and of *Pelargonium* and several other forms, described by Bateson (1919), all of which involve green and white regions of the plants and some of which produce reverse periclinal chimæras, is fundamentally the same as that of graft-hybrids. The manner of origin of these natural chimæras is unknown, but it is quite possible that they arose as somatic mutations.

The case of *Bouvardia* also, as reported by Bateson (1916), is presumably of quite the same order as the examples noted above, though its behavior is strikingly different in detail. Varieties of *Bouvardia* that are maintained true to type by propagation from stem cuttings produce plants with very different flower form, size, and color when propagated by root cuttings. While this behavior is not to be taken as positive proof that these varieties are natural periclinal chimæras, it is quite in keeping with such an assumption. Since in normally produced buds of the stem both the epidermis and the deeper lying tissues are maintained through direct cell lineage, while the roots produced by stem cuttings arise from the plerome and break through the periblem and dermatogen, forming these parts anew, sprouts that develop from the roots must have the genotype of the stele rather than that of the cortex or epidermis.

From the results of critical investigations cited in this account, it is evident that vegetative variations are due to diverse causes. Some are certainly due to somatic mutation of genes; others are as certainly due to chromosome aberrations; and still others have been somewhat definitely shown to involve a vegetative segregation of plastids or other cytoplasmic elements. There are many problems relating to these several types of behavior that are in great need of further critical study both genetic and cytological. The results of future research will depend in large measure on the choice of favorable material. Quantitative data are of the greatest importance

and from this standpoint no material gives more promise of fruitful results than that involving variegation.

LITERATURE CITED

Bateson, W. Root-cuttings, Chimeras and "Sports." *Jour. Genetics,* 6: 75–80. 1916.

—— Studies in Variegation. *Jour. Genetics,* 8: 93–98. 1919.

Baur, Erwin. Das Wesen und die Erblichkeitsverhältnisse der "Varietates albomarginatae hort." Von *Pelargonium zonale. Zeitschr. indukt. Abstamm. Vererb.,* 1: 330–351. 1909.

—— Mutationen von *Antirrhinum majus. Zeitschr. indukt. Abstamm. Vererb.,* 19: 177–193. 1918.

Blakeslee, A. F. A Dwarf Mutation in *Portulaca* Showing Vegetative Reversions. *Genetics,* 5: 418–433. 1920.

Bridges, Calvin B. The Developmental Stages at which Mutations Occur in the Germ Tract. *Proc. Soc. Exp. Biol. and Med.,* 17: 1–2. 1919.

Correns, C. Ueber Bastardirungsversuche mit Mirabilis-Sippen. *Ber. Deutsch. Bot. Gesellsch.,* 20: 594–608. 1903.

—— Zur Kenntnis der scheinbar neuen Merkmale der Bastarde. *Ber. Deutsch. Bot. Gesellsch.,* 23: 70–85. 1904.

—— Vererbungsversuche mit blass(gelb)grünen und buntblättrigen Sippen bei *Mirabilis Jalapa, Urtica pilulifera,* und *Lunaria annua. Zeitschr. indukt. Abstamm. Vererb.,* 1: 291–329. 1909*a*.

—— Zur Kenntnis der Rolle von Kern und Plasma bei der Vererbung. *Zeitschr. indukt. Abstamm. Vererb.,* 2: 331–340. 1909*b*.

—— Der Übergang aus dem homozygotischen in einen heterozygotischen Zustand im selben Individuum bei buntblättrigen und gestreiftbluhenden Mirabilis-Sippen. *Ber. Deutsch. Bot. Gesellsch.,* 28: 418–434. 1910.

deVries, Hugo. The Mutation Theory (translation by J. B. Farmer and A. D. Darbishire). 1910.

East, E. M. The Bearing of Some General Biological Facts on Bud-variation. AMER. NAT., 51: 129–143. 1917.

Emerson, R. A. The Possible Origin of Mutations in Somatic Cells. AMER. NAT., 47: 375–377. 1913.

—— The Inheritance of a Recurring Somatic Variation in Variegated Ears of Maize. AMER. NAT., 48: 87–115. 1914.

—— Genetical Studies of Variegated Pericarp in Maize. *Genetics,* 2: 1–35. 1917.

—— Genetic Evidence of Aberrant Chromosome Behavior in Maize Endosperm. *Amer. Jour. Bot.,* 8: 411–424. 1921.

Frost, Howard B. An Apparent Case of Somatic Segregation involving Two Linked Factors. AMER. NAT., 55: 461–464. 1921.

Gregory, R. P. On Variegation in *Primula sinensis. Jour. Genetics,* 4: 305–321. 1915.

Morgan, T. H. and Bridges, C. B. The Origin of Gynandromorphs. Carnegie Inst. Wash., Pub. 278: 1–122. 1919.

Muller, H. J. Further Changes in the White-eye Series of *Drosophila* and their Bearing on the Manner of Occurrence of Mutation. *Jour. Exp. Zool.,* 31: 443–473. 1920.

Randolph, L. F. A Cytological Study of Some Chlorophyll Types in Maize. *Bot. Gaz.,* 1922. (In press.)